# Photosynthetic Adaptability of Two Fern Species of a Northern Hardwood Forest

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The capacity for acclimation, "the gradual and reversible adjustment of physiology or morphology as a result of changing environmental conditions" (Lincoln, et al., 1982), varies among plant species (Chapin, 1980; Hicks & Chabot, 1985). Fast-growing species of partially shaded habitats have the greatest ability to acclimate to maximize production in shade (Grime, 1981). Shade leaves are generally thinner and have larger leaf areas, lower concentrations on a mass basis and contents on an area basis of RUBISCO and leaf protein, and frequently higher chlorophyll contents but lower chlorophyll concentrations than sun leaves (Björkman & Holmgren, 1963; Ludlow & Wolf, 1975; Boardman, 1977; Hicks & Chabot, 1985). A positive correlation between net photosynthetic rate per unit leaf area and N content has been reported for a variety of plants including woody and herbaceous species (Field & Mooney, 1986; Evans, 1989; Karlsson, 1991; Tuohy, et al., 1991). Higher light-saturated net photosynthetic rates per unit leaf area have been found for sun-grown than shade-grown conspecifics (Björkman & Holmgren, 1963). Seasonal changes in photosynthesis have been reported by Bauer, et al. (1991) for *Dryopteris filix-mas* (L.) Schott.

The present study was undertaken to determine the photosynthetic adaptabilities to sun and shade of two contrasting fern species of a northern hardwood forest. *Dryopteris intermedia* (Muhl. ex Willd.) Gray is a semi-evergreen fern of northern hardwood forest understories in North America, frequently occurring beneath the forest canopy but also found in gaps of recent origin (Siccama, et al., 1970; Hughes & Fahey, 1991). Congeners (*Dryopteris spinulosa* (O.F. Muell.) Watt and *D. marginalis* (L.) Gray) have been described by Sparling (1967) as shade-tolerant. *Dennstaedtia punctilobula* (Michx.) Moore is a summergreen fern frequently occurring in forest gaps and clearings but also found beneath the canopy (Flaccus, 1959; Siccama, et al., 1970; Hughes & Fahey, 1991). We hypothesized that both sun- and shade-grown sporophytes of the competitive, mainly gap-phase species, *Dennstaedtia punctilobula,* would have higher net photosynthetic rates than both sun- and shade-grown sporophytes of the shade-tolerant species, *Dryopteris intermedia.* We also expected that sun-grown sporophytes of each species would have higher net photosynthetic rates and N contents per unit leaf area, but lower N concentrations per unit dry mass than shade-grown sporophytes.

## MATERIALS AND METHODS

Fern sporophytes of each species were collected from the Huntington Forest within the Adirondack Park, New York in August 1991. Six plants (presumably genets) of

Table 1. Characteristics (± SE) of *Dryopteris intermedia* and *Dennstaedtia punctilobula* fern fronds. Mean values of 3 samples unless noted otherwise. * indicates significantly different ($P \leq 0.05$) following $t$ - test.

| Variable | Shade-grown | Sun-grown | $t$ | $df$ | $P$-value |
|---|---|---|---|---|---|
| *Dryopteris intermedia* | | | | | |
| Area ($cm^2$) | 43.40±2.47 | 38.33±1.10 | -1.88 | 4 | 0.13 |
| Dry mass (g) | 0.153±0.004 | 0.173±0.006* | 2.72 | 4 | 0.05 |
| Dry mass/area ($g/cm^2$) | 0.0035±0.0002 | 0.0045±0.00006* | 4.97 | 4 | 0.01 |
| C concentration (% dry mass) | 47.61±0.17 | 47.81±0.18 | 0.81 | 4 | 0.46 |
| C content ($mg/cm^2$) | 168.28±9.33 | 215.14±1.99* | 4.91 | 4 | 0.01 |
| N concentration (% dry mass) | 2.45±0.15 | 2.06±0.27 | -1.29 | 4 | 0.27 |
| N content ($mg/cm^2$) | 8.68±0.83 | 9.24±1.12 | 0.40 | 4 | 0.71 |
| *Dennstaedtia punctilobula* | | | | | |
| Area ($cm^2$) | 29.08±3.32 | 25.08±1.98 | -0.82 | 4 | 0.46 |
| Dry mass (g) | 0.046±0.010 | 0.075±0.009 | 2.15 | 4 | 0.10 |
| Dry mass/area ($g/cm^2$) | 0.0016±0.0002 | 0.0029±0.0002* | 4.89 | 4 | 0.01 |
| C concentration (% dry mass) | 46.93±0.04 | 47.62±0.52[a] | 1.03 | 3 | 0.38 |
| C content ($mg/cm^2$) | 79.78±9.31 | 138.30±11.42* | 3.59 | 3 | 0.04 |
| N concentration (% dry mass) | 2.49±0.24 | 2.25±0.39[a] | -0.45 | 3 | 0.68 |
| N content ($mg/cm^2$) | 4.19±0.09 | 6.62±1.53 | 1.23 | 3 | 0.31 |

[a]n = 2, limited sample

*Dryopteris intermedia* were collected from beneath a forest canopy and six plants of *Dennstaedtia punctilobula* were collected from a nearby clearing. The plants were potted in organic soil in which the plants occurred and transferred to a greenhouse.

Three plants of each species were placed in direct sunlight and three plants of each species were placed in shade. The plants were watered to field capacity twice daily by an automated drip-irrigation system. Typical shade and sun irradiance levels were 62 and 945 $\mu mol\ m^{-2}s^{-1}$ at solar noon on a clear day and 27 and 92 $\mu mol\ m^{-2}s^{-1}$ on a cloudy day, respectively, and compare well with field measurements (Brach, unpublished data). The ferns were allowed to acclimate and grow for two months prior to gas exchange measurements.

Using a steady-state differential gas analysis apparatus, carbon dioxide exchange measurements were made on the most recently developed, fully-expanded frond of each plant that developed during the acclimation period. Since all fronds which developed after transfer were sterile, measurements were made only on sterile fronds. System design and materials followed standard criteria (Bloom, et al., 1980). Conditions chosen and maintained during measurement were a temperature of 25°C, 85% relative humidity, and 350$\mu l\ l^{-1}$ $CO_2$. Light was supplied by a 1.5 kW xenon arc lamp. Photosynthetic photon flux density (PPFD) was increased progressively to five levels by removing neutral density filters.

Following gas exchange measurement of each frond, the portion of the frond that was in the cuvette was excised and its leaf area measured using an area meter (Model LI-3000 with LI-3050A conveyer, Li Cor Inc.). Fronds were dried to constant mass at 65°C. Carbon and N concentrations were determined using a CHN analyzer (Model 240C,

Table 2. Repeated measures ANOVAs for net photosynthetic rate per unit leaf area and per unit dry mass for the two fern species.

| Source | *MS* | *df* | *F* | *P* | (H-Fp[a]) |
|---|---|---|---|---|---|
| Net photosynthetic rate per unit leaf area | | | | | |
| species | 24.81 | 1 | 3.97 | 0.0813 | |
| treatment | 7.25 | 1 | 1.16 | 0.3125 | |
| spp. X trmt. | 9.14 | 1 | 1.46 | 0.2607 | |
| between subject | 6.26 | 8 | | | |
| PPFD level | 0.78 | 4 | 8.83 | | 0.0030 |
| spp. X level | 0.30 | 4 | 3.38 | | 0.0623 |
| trmt. X level | 0.24 | 4 | 2.72 | | 0.0990 |
| spp. X trmt. X level | 0.04 | 4 | 0.49 | | 0.6135 |
| within subject | 0.08 | 32 | | | |
| Net photosynthetic rate per unit dry mass | | | | | |
| species | 402685.95 | 1 | 27.53 | 0.0008 | |
| treatment | 223260.00 | 1 | 15.26 | 0.0045 | |
| spp. X trmt. | 161160.20 | 1 | 11.02 | 0.0106 | |
| between subject | 14624.34 | 8 | | | |
| PPFD level | 1289.21 | 4 | 10.57 | | 0.0018 |
| spp. X level | 721.59 | 4 | 5.92 | | 0.0150 |
| trmt. X level | 246.54 | 4 | 2.02 | | 0.1704 |
| spp. X trmt. X level | 122.85 | 4 | 1.01 | | 0.3818 |
| within subject | 121.63 | 32 | | | |

[a] Huynh – Feldt corrected level of significance

Perkin-Elmer) and contents calculated. Two analytical replicates were averaged per sample.

For each species, Student's *t*-tests (SAS, 1985) for each species were used to determine if leaf area, dry mass, dry mass per unit leaf area; C and N concentrations and contents were significantly different between growing conditions. Net photosynthetic rates of both species per unit leaf area and per unit dry mass were analyzed by repeated measures ANOVAs (SAS, 1985; Potvin & Charest, 1991). The main effects tested were species, treatment (growing conditions), and PPFD level. Species, treatment and species X treatment were considered as between-subject effects, while PPFD level was considered a within-subject factor.

## Results

Morphological characteristics of the ferns grown under contrasting greenhouse conditions are presented in Table 1. In both species, sun-grown plants had significantly higher dry mass per unit leaf area than shade-grown plants. Sun leaves of sun-grown ferns of both species were yellow-green as compared to darker green shade leaves of shade-grown ferns.

Fronds of shade-grown ferns had generally higher, but not significantly different ($P > 0.05$), N concentrations and generally lower, but not significantly different ($P > 0.05$), N contents compared to fronds of sun-grown ferns. Fronds of sun-grown ferns had significantly higher C contents than fronds of shade-grown ferns (Table 1).

*Dennstaedtia punctilobula* had higher net photosynthetic rates per unit dry mass than *Dryopteris intermedia* (Table 2, Fig. 1), but not per unit leaf area (Table 2, Fig. 2). Shade-grown *Dennstaedtia punctilobula* had significantly higher net photosynthetic rates per

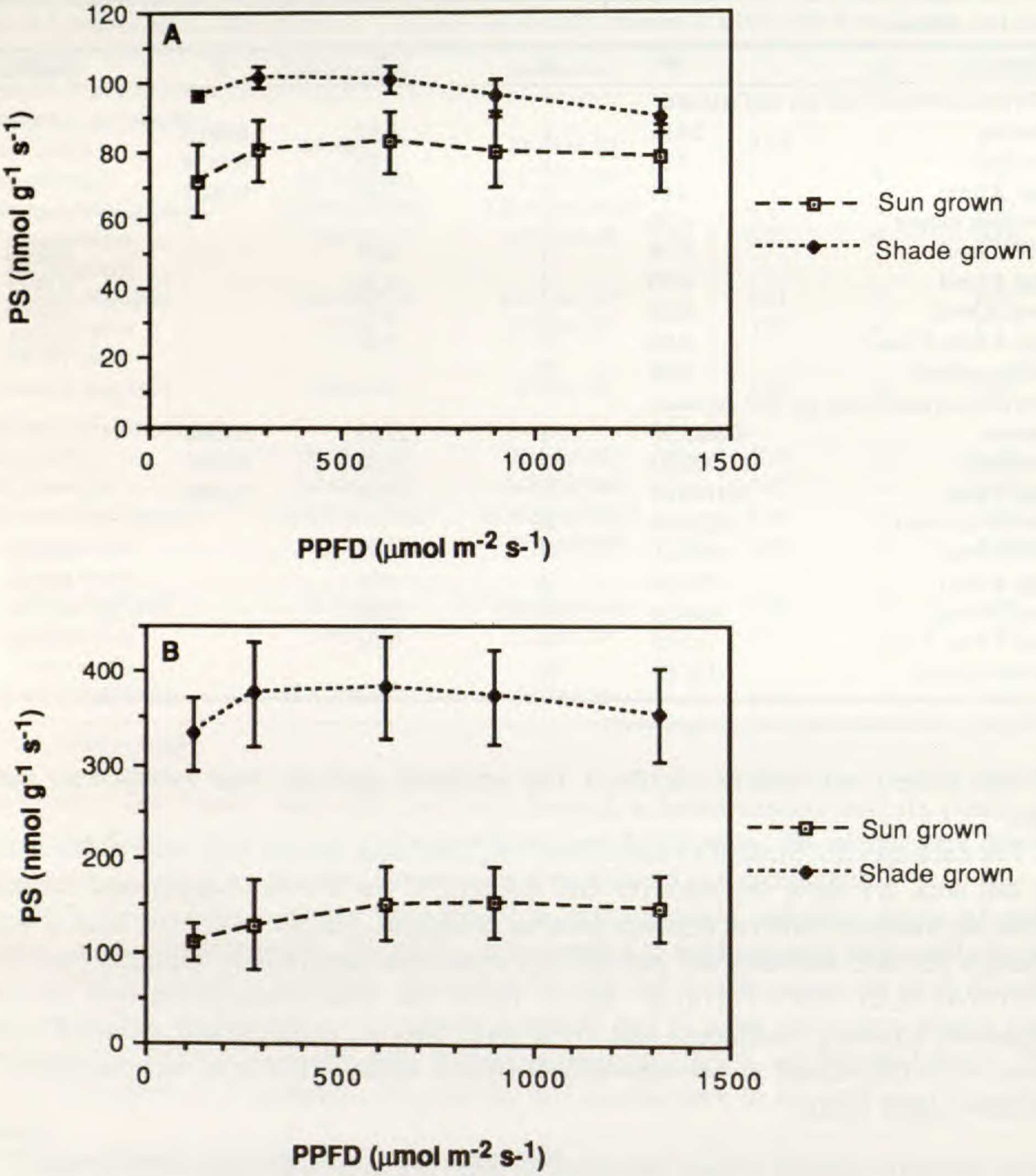


Fig. 1. Mean net photosynthetic rate (PS) (± SE) per unit dry mass of A) *Dryopteris intermedia* and B) *Dennstaedtia punctilobula* for five levels of photon flux density (PPFD). Marks represent mean values of 3 samples.

unit dry mass than sun-grown conspecifics over all PPFD levels used (Fig. 1b). Net photosynthetic rates per unit leaf dry mass were significantly affected by species, treatment, species X treatment, PPFD level, and species X PPFD level (Table 2). Species, treatment, and the species X treatment interaction accounted for 50, 28, and 20% of the total variance, respectively. Additionally, shade-grown *Dennstaedtia punctilobula* had higher net photosynthetic rates per unit leaf area than sun-grown conspecifics at the lowest PPFD level used (Fig. 2b).

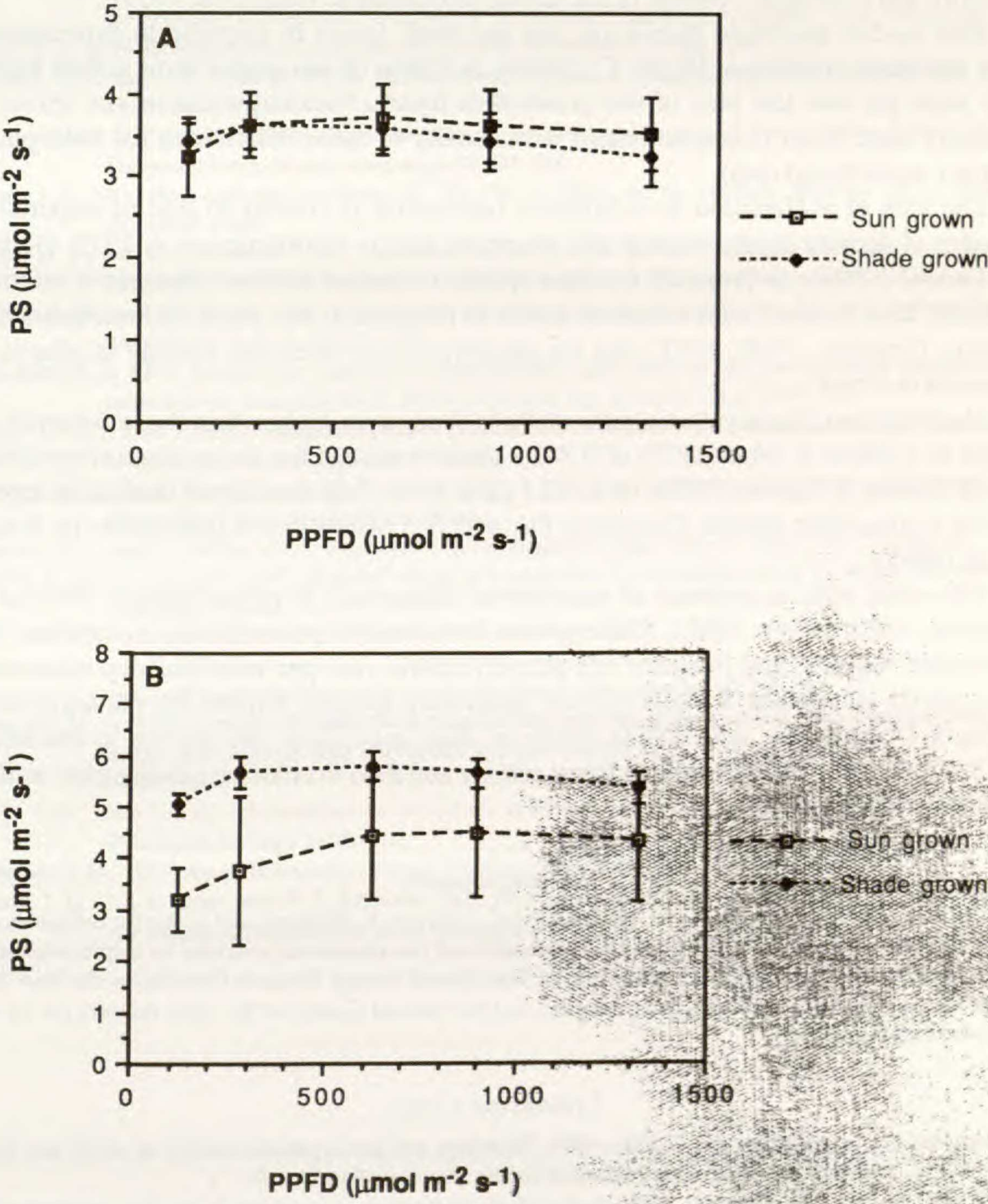


Fig. 2. Mean net photosynthetic rate (PS) (± SE) per unit leaf area of A) *Dryopteris intermedia* and B) *Dennstaedtia punctilobula* for five levels of photon flux density (PPFD). Marks represent mean values of 3 samples.

## Discussion

Shade-grown *Dennstaedtia punctilobula* had higher net photosynthetic rates per unit dry mass than *Dryopteris intermedia*. However, contrary to our expectations, shade-grown *Dennstaedtia punctilobula* had higher net photosynthetic rates than sun-grown conspecifics. Plausible reasons for this response include adaptability of shade leaves to utilize periodic sunflecks (Chazdon & Pearcy, 1991; Gildner & Larson, 1992a), higher chlorophyll contents in shade leaves than sun leaves (Boardman, 1977), and photoinhibitory and chloroplast damage in sun leaves (Björkman & Holmgren, 1963).

Both species developed phenotypic sun and shade leaves in response to experimental sun and shade conditions. Higher C contents in fronds of sun-grown ferns reflect higher dry mass per unit leaf area of sun-grown fern fronds. Nutrient stress in sun leaves is unlikely since frond N concentrations were similar to those determined for field plants (Brach, unpublished data).

The lack of acclimation in *Dryopteris intermedia* is similar to that of understory species of densely shaded tropical and temperate forests (Björkman, et al. 1972; Gildner & Larson, 1992b). As proposed for other species of shaded habitats, *Dryopteris intermedia* may have evolved semi-evergreen leaves in response to low water and nutrient availability (Sobrado, 1986; 1991) and for photosynthesis when the canopy is absent or reduced in winter.

Maximum net photosynthetic rates of these ferns were higher than those reported for ferns by Ludlow & Wolf (1975) of 0.7–1.3 $\mu$mol $m^{-2}s^{-1}$ and for *Polypodium virginianum* L. by Gildner & Larson (1992b) of 1.2–2.5 $\mu$mol $m^{-2}s^{-1}$, and were lower than those reported for a congeneric species, *Dryopteris filix-mas* (L.) Schott of 8–9 $\mu$mol $m^{-2}s^{-1}$ by Bauer, et al. (1991).

This study adds to evidence of successional differences in photosynthesis (Bazzaz & Carlson, 1982; Koike, 1988). Shade-grown *Dennstaedtia punctilobula,* a vigorous gap colonizer species, had a higher net photosynthetic rate per unit leaf dry mass than *Dryopteris intermedia,* a shade-tolerant understory species. Higher net photosynthetic rates of *Dennstaedtia punctilobula* grown in shade may allow this species to efficiently utilize low light when beneath the forest canopy and then to colonize canopy gaps as they become available.

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